

CHARACTERISTICS AND DYNAMICS OF AN UPLAND MISSOURI OLD-GROWTH FOREST

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Abstract: We describe the structure, composition, and dynamics of Schnabel Woods, an 80-acre mixed mesophytic old-growth stand located in the loess-covered River Hills adjoining the Missouri River floodplain in central Missouri. In 1982 all trees on a 1.5-ac northwest-facing plot and a 1.5-ac southeast-facing plot were mapped and measured. In 1992 we remeasured those plots to observe current conditions and changes in species composition and stand structure over time. In 1992 density was 381 trees/acre, basal area was 124 ft²/ac, and the mean dbh was 5.2 in (for trees $\geq$ 0.8 in dbh). The stand was fully stocked at 101%. Between 1982 and 1992 tree density decreased by 11% while total basal area remained constant. However, basal area did shift among species groups; basal area for northern red oak and white oak increased by 10% while basal area for other species groups remained the same or decreased. The volume of down wood with a minimum diameter $\geq$ 4 in averaged 338 ft³/ac over both plots. Litter dry weight averaged 4.9 tons/ac and was significantly greater on the southeast than the northwest aspect. Northern red oak dominated the overstory, but maple dominated the understory and comprised 67% of the ingrowth. Current dynamics are driven by fine-scale treefall gaps, where maples are replacing oaks.

INTRODUCTION

Schnabel Woods is one of the few remaining remnant old-growth tracts in the loess-covered River Hills of Boone County, within Missouri's Ozark Border Natural Division (Thom and Wilson 1980). Less than 0.07% of the original old-growth forest in the central hardwoods region remains (Parker 1989), and in Missouri only 0.05% of the existing forest is classified as old-growth (Shifley 1994). Remnant old-growth tracts such as Schnabel Woods are of interest because they are rare, but more importantly they provide the best available information about probable long-term patterns of development and succession in the surrounding second-growth forests. To the extent that silvicultural practices resemble gap dynamics, old-growth can also reveal successional tendencies in managed stands (Abrams and Scott 1989). Moreover, old-growth forests are at one end of the spectrum of forest development. As such they provide an ecological frame of reference from which to quantitatively evaluate the current structure, composition, diversity, and dynamics of second-growth forests.

Schnabel Woods was first studied by Kucera and McDermott (1955) who reported that dominant white oaks⁵ averaged 165 years old with dbhs (diameter at breast height) between 27 and 31 in. The species with the highest importance values were sugar maple, northern red oak, and basswood. At that time they noted that the tract was "representative of the original forest" and Kucera (personal communication, Nov. 94) found no evidence of significant anthropogenic disturbance at the time of his study.

Since Boone County was first surveyed in 1816-17, the species composition of Schnabel Woods appears to have gradually shifted from predominantly oak to predominantly maple. Wuenscher and Valiunas's (1967) study of

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⁵Scientific names of all species are given in Table 4.

surveyor records for the River Hills of Boone County indicates that in the first quarter of the 19th century, the importance value of white oak exceeded that of sugar maple. Similarly, Howell and Kucera's (1956) study of surveyor records for Boone County, Missouri, showed that 58% of the witness trees in the original land surveys were *Quercus* spp., primarily white oak and bur oak (39% and 16%, respectively). By 1955, Kucera and McDermott (1955) reported that the importance value of sugar maple was almost twice that of red oak. Species with lower shade tolerance followed in importance ranking: *Tilia americana*, *Ulmus* spp., *Fraxinus* spp., and *Quercus* spp. The transition from an oak-dominated forest to one with more shade tolerant species, particularly sugar maple, is consistent with findings for numerous other mesic mature and old-growth remnants in the central hardwood region (e.g., Nigh and others 1985, Schlesinger 1989, Shotola and others 1992, Wuenscher 1967, Lindsey 1962, Parker and Leopold 1983, McGee 1984, Barton and Schmelz 1987).

In this paper we describe the current structure, composition, growth, and mortality at Schnabel Woods. We compare the structure and composition of a northwest-facing and southeast-facing aspect in Schnabel Woods and we examine the dynamics over a ten-year interval. In addition, we compare our findings with Kucera and McDermott's (1955) compositional study.

METHODS

Study Area

Schnabel Woods is located approximately 2.5 miles southeast of McBaine in Boone County, Missouri (Figure 1). The 80-acre tract sits in the River Hills immediately east of and above the Missouri River floodplain. The deep Menfro loess soils are capable of supporting rich mesic upland forest and diverse ephemeral ground flora (Kucera and McDermott 1955). With the exception of this tract, the surrounding area has been extensively cut over, grazed, and/or farmed. During the 1940s light selective logging of some high quality timber took place in or around Schnabel Woods (Tom Douglas⁶, personal communication, 1994). In 1954 the tract was deeded to the University of Missouri as an arboretum

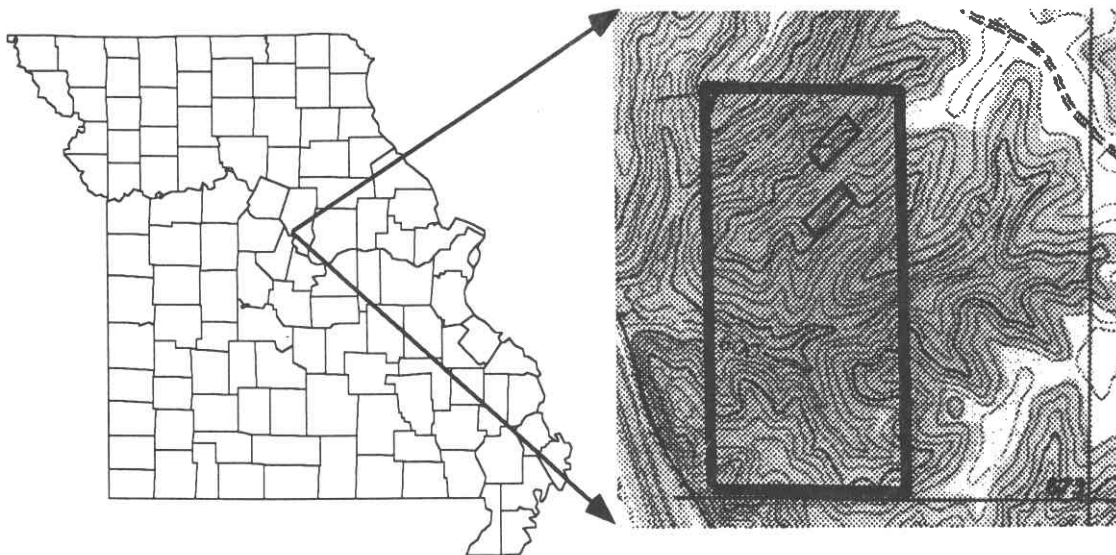


Figure 1. Boundary of Schnabel Woods showing approximate plot locations, Boone County, Missouri. Schnabel Woods legal description is W $\frac{1}{2}$, SE $\frac{1}{4}$, Sect. 7, T48N, R13W.

⁶Tom Douglas owns the farm adjacent to Schnabel Woods and is a long-term resident of the area.

and demonstration woods. Since acquisition by the University of Missouri, no active vegetative management has occurred. In 1978 the tract was designated a state natural area. Three small fires have been documented as well as a few brief incidents of grazing by stray cattle from the surrounding pastures.

Field Procedure

In 1982 Chaplin and students mapped all live trees ≥ 0.8 -in (2.0-cm)⁷ dbh in two 1.5-ac (0.6-ha) plots. To compare the current composition and structure of two separate aspects, one plot was located on the major northwest-facing slope in the tract; the other plot was placed on the opposite southeast-facing slope on the same ridge (Figure 1). The plots have a vertical relief of approximately 100 ft and a slope of approximately 35%. Although placement of plots was not random, we believe these plots are representative of Schnabel Woods.

Species and dbh were recorded for each live tree ≥ 0.8 -in dbh. Stem maps for each plot were created by subdividing each plot into sixty 0.025-ac (100-m²) square subplots and recording the Cartesian coordinates of each tree within its respective subplot. In 1992 we relocated the plots and measured dbh, crown class (dominant, codominant, intermediate, overtopped), crown ratio percent, and status (live, dead, ingrowth) for each tree ≥ 0.8 in dbh. On every second subplot (half the total sample area) the number of cavities in each individual tree was recorded by minimum opening size (1-2, 2-4, or 4+ in; 2-5, 5-10, or 10+-cm). Ingrowth during the ten-year period was defined as any live tree (≥ 0.8 in) present in 1992 that was not recorded in 1982. In 1992 down woody material ≥ 4 -in (10 cm) in diameter was recorded by length and midpoint diameter on the main plots. Volume of each piece of down wood was computed as the volume of a cylinder, and each piece was classified into one of five decay stages following the classification system of Maser and others (1979). Within each main plot, forest floor litter was collected from four systematically established locations. Each litter sample totaled 10.8 ft² (1.0-m²) in area, and was collected as the composite of eight 1.4-ft² (0.125-m²) subplots. At four of the litter subplots, soil was collected to a depth of 20 cm and sent to an independent lab for organic matter determination. In 1982 soil samples were also collected and analyzed for percent organic matter by the weight loss on combustion method.

Analysis

Density (i.e. number of trees per unit area), basal area, and stocking were calculated for each tree and summed to obtain plot means or class summaries. Stocking was computed using the tree area ratio equations of Gingrich (1967) and Stout and others (1987). Trees were grouped into 2-in (5-cm) dbh classes to observe and compare dbh frequency distributions. Species groups (Table 1) were created to clarify trends for those species which were relatively rare. Contingency table analysis (chi-square test) was used to test for differences in the diameter distributions and species groups distributions between aspects. Student's t-test was used to test for differences in dry litter weight between aspects. Spatial patterns were tested using Ripley's K(t) or K12(t) (Diggle 1981, Ripley 1977). The K(t) function uses distances between mapped objects (e.g. trees) to measure the degree of clumping (attraction), regularity (repulsion), or randomness (independence) among individuals.

RESULTS

Structure

In 1992 the average density of live tree and shrub stems ≥ 0.8 in dbh across both plots was 381 trees/ac (942/ha). At 452 trees/ac (1116 /ha), density on the southeast aspect was 50% greater than that observed on the northwest aspect. However, the basal area on the southeast aspect was 10 ft²/ac (2 m²/ha) less than on the northwest aspect (Table 2).

⁷A full set of metric equivalents is given following Literature Cited.

Table 1. Species groups used to classify trees at Schnabel Woods.

Species Group	Included species
Ash	<i>Fraxinus americana</i> , <i>F. quadrangulata</i> , <i>F. pennsylvanica</i>
Maple	<i>Acer saccharum</i> , <i>A. nigrum</i>
Red oak	<i>Quercus rubra</i> , <i>Q. shumardii</i>
White oak	<i>Q. alba</i> , <i>Q. muehlenbergii</i>
Hickory	<i>Carya laciniosa</i> , <i>C. texana</i> , <i>C. cordiformis</i>
Elm	<i>Ulmus rubra</i> , <i>U. americana</i>
Basswood	<i>Tilia americana</i>
Understory	<i>Cornus florida</i> , <i>Ostrya virginiana</i> , <i>Asimina triloba</i> , <i>Cercis canadensis</i>
Mesic	<i>Juglans nigra</i> , <i>Celtis</i> spp., <i>Gymnocladus dioica</i>

Table 2. Summary of mean stand characteristics observed at Schnabel Woods, 1982-1992.

Characteristic	Live trees (trees/ac)	Live basal area (ft ² /ac)	Mean dbh (in)	Stocking %	Standing dead basal area (ft ² /ac)
1982 Total					
Combined	452	124	4.6	102	--
NW	367	124	5.3	103	--
SE	539	123	4.2	101	--
1992 Total					
Combined	381	124	5.2	101	9.37
NW	310	129	6.0	104	6.32
SE	452	119	4.6	97	12.4
Net change 1982-1992					
Combined	-71	0	0.6	-1	
NW	-57	5	0.7	1	--
SE	-87	-4	0.4	-4	--
Relative change 1982-1992					
Combined	-16%	0%	13%	-1%	--
NW	-15%	4%	13%	1%	--
SE	-16%	-3%	10%	-4%	--

The combined diameter distribution for both aspects has a reverse J-shape (Figure 2) and 86% of the trees are < 10 in (25 cm) dbh. Interestingly, the shapes of the diameter distributions for live and dead trees are very similar, but there is a 10-fold difference in densities. This is consistent with observations for other old-growth sites in Missouri (Shifley and others 1995).

Diameter distributions were significantly different on the two aspects (chi-square, $p = 0.004$, 15 d.f.). (Figure 3). The southeast aspect had almost twice as many stems < 10-in dbh than the northwest aspect.

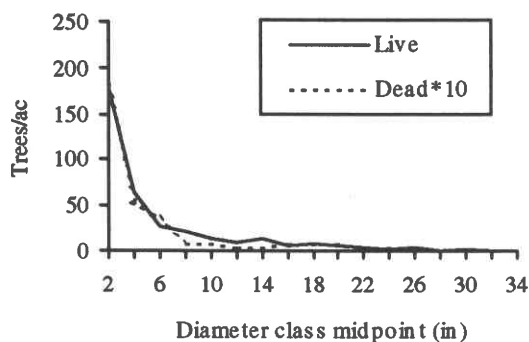


Figure 2. Number of live and dead (scaled by a factor of 10) trees/ac in 2-in dbh classes at Schnabel Woods, 1992.

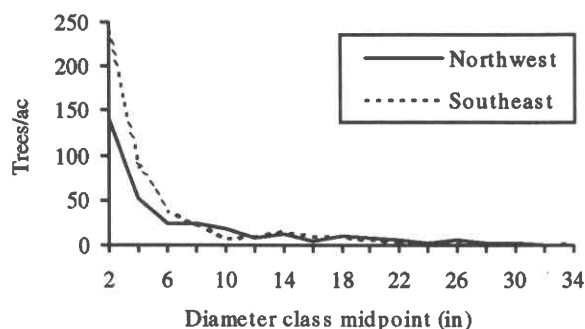


Figure 3. Number of live trees/ac by aspect in 2-in dbh classes at Schnabel Woods, 1992.

Five percent of the standing trees (live or dead) had natural or excavated cavities. The probability of a tree of a given dbh having one or more cavities increased linearly from 8% for a 4-in (10-cm) dbh tree to 30% for a 30-in dbh tree.

Down wood ≥ 4 in dbh on the two plots averaged 563 ft³/ac. Most of this volume was in the intermediate decomposition class (Table 3). The number of pieces decreased exponentially with increasing volume per piece (Figure 4). The largest piece of down wood we observed had a volume of 88 ft³. There were relatively few pieces shorter than 3 ft.

Table 3. Volume of down wood ≥ 4 in diameter at Schnabel Woods, 1992. Decomposition classes follow Maser and others (1979).

Decomposition class	Defining characteristics	Volume (ft ³ /ac)
Class 1	Round log, bark intact, small twigs present, log elevated on support points	0
Class 2	Round log, bark intact, twigs absent, log elevated on support points	130
Class 3	Round log, traces of bark, twigs absent, log sagging near ground	286
Class 4	Round to oval log, bark absent, twigs absent, log entirely on ground	101
Class 5	Oval log, bark absent, twigs absent, log entirely on ground	46
Total		563

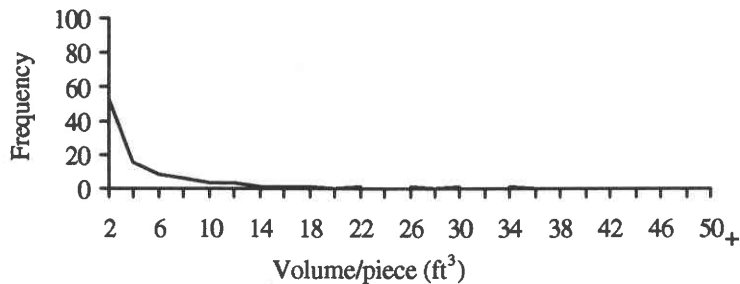


Figure 4. Frequency of down dead wood by volume (ft³) class midpoint for Schnabel Woods, 1992. Note that graph stops at 50 ft³ but the largest piece was 89 ft³.

Soil organic matter averaged 8.6% in 1982 and 8.5% in 1992. No difference was observed between measurement intervals (t-test, $p=.47$, 20 d.f.), between aspects in 1982 (t-test, $p=.47$, 4 d.f.), or between aspects in 1992 (t-test, $p=.25$ 14 d.f.).

Dry weight of litter on the forest floor averaged 4.9 tons/ac (1.1 metric tons/ha). The mean mass of litter was significantly greater on the southeast (5.6 tons/ac) than the northwest plot (4.2 tons/ac) (t-test, $p = 0.002$, 6 d.f.).

Species Composition

Twenty-two tree species were observed at Schnabel Woods in 1992: 19 on the northwest aspect and 17 on the southeast aspect (Table 4). Eight species on the northwest aspect and ten on the southeast aspect had fewer than five stems. In addition, three vine species were observed on both aspects.

Sugar maple was by far the most common species on both aspects at Schnabel Woods, comprising 74% of the trees and 35% of the basal area (Table 4). In terms of importance value, northern red oak was the second most dominant species. The magnitude of the difference between a species' relative basal area and relative density (Table 4) gives some indication of that species' relative size structure. For example, the relative basal area for northern red oak is approximately 10 times its relative density, while sugar maple has a relative basal area that is half of its relative density. This indicates that northern red oaks are, on average, substantially larger in diameter than sugar maples. Dominance of northern red oak in the overstory and sugar maple in the understory is clearly illustrated by Figure 5, which shows the relative basal area by crown class. Maples comprise over 80% of the basal area at lower crown positions but < 20% in the dominant crown class. Northern red oak accounts for 64% of the basal area in the dominant crown class but is absent in the overtopped crown class. Differences among species by aspect were most notable in the smaller size classes. Maple comprised 93% of trees ≤ 10 in dbh on the southeast aspect, but only 67% of the trees on the northwest aspect (Table 5). The understory species group (*Cornus florida*, *Ostrya virginiana*, *Asimina triloba*, and *Cercis canadensis*) comprised an additional 19% of the stems ≤ 10 in dbh on the northwest aspect.

Compared to importance values reported for Schnabel Woods nearly 30 years earlier by Kucera and McDermott (1955), the importance of sugar maple increased by 20%, primarily at the expense of basswood (Table 4). However, given that the field sample by Kucera and McDermott did not necessarily coincide with our sample site, there is some ambiguity associated with interpreting such differences.

Table 4. Importance percentages for Schnabel Woods, northwest and southeast aspects combined.

Species	Aspect where spp. occurs	1992			1955
		Relative density	Relative basal area	Importance value	Importance value ^a
Sugar maple (<i>Acer saccharum</i>)	NW, SE	74.2	35.1	54.7	35
Northern red oak (<i>Quercus rubra</i>)	NW, SE	2.9	27.3	15.1	19
Chinquapin oak (<i>Quercus muehlenbergii</i>)	NW, SE	3.3	11.4	7.3	6
American basswood (<i>Tilia americana</i>)	NW, SE	1.9	5.9	3.9	18
White oak (<i>Quercus alba</i>)	NW, SE	0.9	5.2	3.0	0
Slippery or red elm (<i>Ulmus rubra</i>)	NW, SE	2.8	2.1	2.5	0
White ash (<i>Fraxinus americana</i>)	NW, SE	1.8	3.1	2.4	0
Black maple (<i>Acer nigrum</i>)	NW	1.5	2.3	1.9	0
Flowering dogwood (<i>Cornus florida</i>)	NW	3.5	0.3	1.9	4
Shagbark hickory (<i>Carya texana</i>)	NW, SE	1.1	1.7	1.4	0
Eastern hophornbeam (<i>Ostrya virginiana</i>)	NW, SE	2.6	0.2	1.4	4
Green ash (<i>Fraxinus pennsylvanica</i>)	NW, SE	0.5	1.9	1.2	4
American elm (<i>Ulmus americana</i>)	NW, SE	0.8	1.0	0.9	6
Kentucky coffeetree (<i>Gymnocladus dioicus</i>)	NW, SE	0.4	0.7	0.6	0
Shellbark hickory (<i>Carya laciniosa</i>)	SE	0.2	0.6	0.4	0
Pawpaw (<i>Asimina triloba</i>)	NW	0.7	0.0	0.4	0
Shumard oak (<i>Quercus shumardii</i>)	SE	0.1	0.6	0.3	0
Hackberry (<i>Celtis</i> spp.)	NW, SE	0.4	0.3	0.3	0
Black walnut (<i>Juglans nigra</i>)	NW	0.2	0.3	0.3	0
Blue ash (<i>Fraxinus quadrangulata</i>)	NW, SE	0.2	<0.1	0.1	0
Eastern redbud (<i>Cercis canadensis</i>)	SE	0.1	<0.1	0.1	0
Bitternut hickory (<i>Carya cordiformis</i>)	NW	0.1	<0.1	<0.1	4

Importance value are computed as {(relative density + relative basal area)/2}.

^aAdapted from Kucera and McDermott (1955)

Table 5. Relative density of live trees < 10 in dbh in each species group by aspect.

Group	Northwest	Southeast
Maple	67.4	93.2
Understory	19.0	0.7
Elm	7.9	1.0
Ash	2.6	1.0
Mesic	1.3	0.5
White oak	0.8	1.7
Hickory	0.5	1.2
Basswood	0.5	0.7

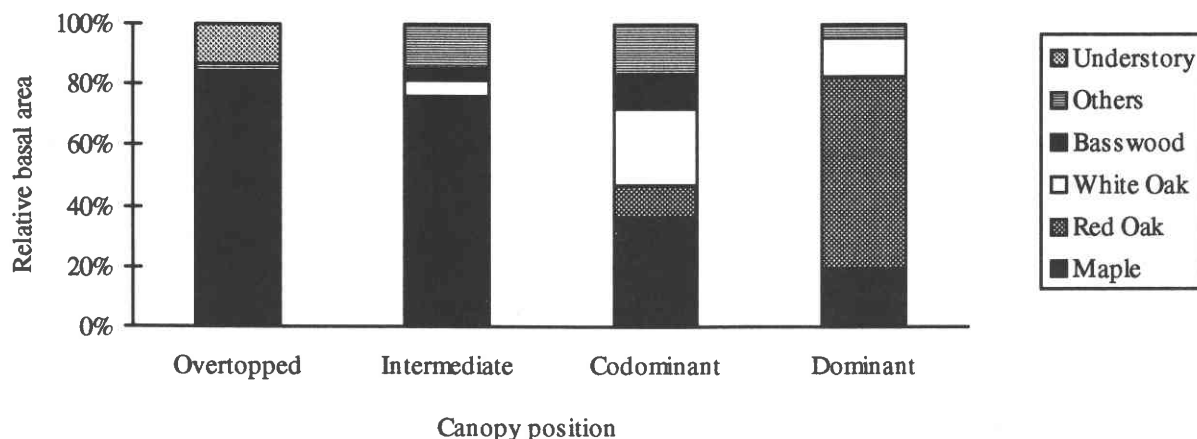


Figure 5. Relative basal area by canopy position at Schnabel in 1992. Note that “others” includes the hickory, ash, elm, and mesic species groups.

The number of trees by species group was significantly different between the two aspects (chi-square test, $p \leq 0.001$, 8 d.f.). Overall, more trees in the ash, elm, red oak, and understory species groups were found on the northwest aspect while maple and white oak species groups were more prevalent on the southeast aspect. Basswood had approximately the same number of stems on both aspects. Interestingly, only 4 stems (0.7 trees/ac) consisting of two species (eastern hophornbeam (3) and redbud (1)) were observed in the understory group on the southeast aspect while 73 stems (49 trees/ac) consisting of three species (flowering dogwood (39), eastern hophornbeam (26) and pawpaw (8)) were on the northwest side.

Forest Dynamics (1982-1992)

Basal area and stocking remained virtually unchanged over the ten-year period at 124 ft²/ac and 101%, respectively (Table 2). However, the density of live trees decreased by 16%, from 452 to 381 trees/ac. There were shifts in the relative importance of species. Although basal area remained constant, the basal area of the oak species groups increased by 10% while the remaining species groups either decreased or did not change (Figure 6).

Individual-tree diameter growth rates varied considerably among species and by crown class for a given species (Table 6). Dominant and codominant trees grew at least twice as fast as intermediate and overtopped trees for all species. The majority of northern red oaks were dominants or codominants; whereas, the majority of sugar maples were overtopped or intermediate.

Mortality rates were lowest for the oaks and maples and highest for the understory species (Table 7). The low mortality rate for maple is consistent with its high shade tolerance and ability to persist for long periods in a suppressed state. The relatively low mortality rate for oaks can be partially attributed to their exclusive position in dominant or codominant canopy classes. However, we have observed numerous northern red oak treefalls outside the plots, suggesting that overall mortality rates for northern red oaks across the entire tract may be higher than observed in our study area. We performed a brief “pilot study” and censused 56 gaps in a 20-ac 8-ha block encompassing the plots, and maples dominated the midstory in 82% (46) of these gaps. Due to few observations, meaningful mortality rates could not be calculated for individual crown classes. The high annual mortality rate for the understory species group reflects its characteristic high turnover rate as these trees struggle to maintain a foothold in the lower canopy strata. Spatial analysis showed that dead trees were randomly distributed throughout all distance classes (Ripley’s $K(t)$, $p > 0.05$) on both aspects.

Table 6. Tree diameter growth (inches per decade) by species and crown class at Schnabel Woods, 1982 to 1992.

Species group	Crown class				Average of all crown classes
	Overtopped	Intermediate	Codominant	Dominant	
Northern red oak	--	--	1.3	1.9	1.7
Basswood	0.0	0.5	1.2	--	1.0
Mesic	--	0.6	1.5	0.7	1.0
White oak	0.1	0.4	1.1	1.3	1.0
Elm	0.8	0.6	1.5	--	0.9
Ash	0.2	0.6	1.1	1.7	0.9
Maple	0.2	0.4	0.8	0.9	0.4
Hickory	0.0	0.2	0.8	0.0	0.4
Understory	0.2	0.7	0.0	0.0	0.2
Average	0.2	0.4	1.1	1.5	0.5

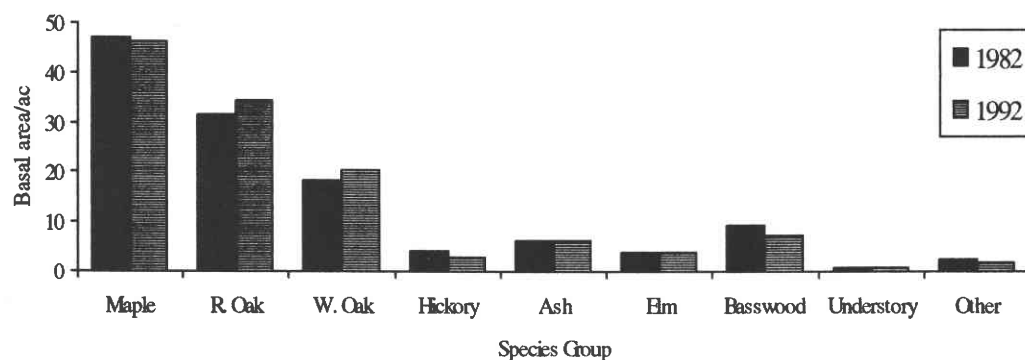


Figure 6. Basal area by species group in 1982 and 1992.

Table 7. Annual mortality rate by species group at Schnabel Woods during the 1982-1992 interval.

Species group	Annual mortality rate (%)
Understory	6.3
Basswood	6.0
Hickory	5.7
Ash	5.4
Elm	5.1
Mesic	5.0
Maple	2.3
Northern red oak	1.4
White oak	1.0
Average	2.8

Ingrowth (trees crossing the 0.8-inch dbh threshold) over the remeasurement interval consisted of 83 trees/ac and 1 ft²/ac of basal area. Ingrowth trees were primarily sugar maple (67%), dogwood (8%), slippery elm (7%), hophornbeam (6%), and pawpaw (5%). Of these species, only maple and elm are capable of becoming part of the overstory, and elm usually succumbs to Dutch elm disease before becoming established as a dominant tree. A single chinquapin oak was the only oak ingrowth observed for the 10-year period.

Small maples, including ingrowth, were highly clumped on both aspects (Ripley's $K(t)$, $p < 0.05$), but there was no strong spatial association (Ripley's $K_{12}(t)$, $p > 0.05$) with overstory trees of any species. There was a tendency for small maples (< 2.0 in dbh) to be clumped under large oaks (> 10 in dbh); however, it was only statistically significant on the northwest aspect. In contrast, small maples tended to be negatively associated with large maples (> 10 in dbh), but again, this was not significant.

DISCUSSION

The differences observed between aspects at Schnabel Woods were substantial, and greater than we would have expected prior to conducting the inventory. Although northeast- and southwest-facing slopes present large differences in environmental conditions, northwest- and southeast-facing slopes are generally expected to present more moderate or neutral environmental conditions (Hartung and Lloyd 1969). The southeast slope at Schnabel Woods had 170 more trees/ac than the northwest slope, but the basal area was 10 ft²/ac less and the mean dbh was 1.4 in less on the southeast slope than on the northwest slope. This pattern is generally indicative of lower site quality and corresponding slower development. A further indication of site quality differences is the mass of forest floor litter which was 38% higher on the southeast slope. The lower value on the northwest slope is indicative of more mesic conditions and a higher rate of litter decomposition.

Large volumes of standing dead and down wood are often associated with old-growth forests (e.g. Parker 1989, Martin 1992). The 10-to-1 ratio of live to dead trees at Schnabel Woods is a phenomenon that has been observed in other old-growth and mature second-growth forests (Shifley and others 1995). At 563 ft³/ac, total volume of down wood was 90 ft³/ac greater than observed at two xeric old-growth sites in southern Missouri (Shifley and others 1995), but well below the 683 ft³/ac (for logs > 7.9 in in diameter) observed by Mueller and Liu (1991) for a mixed mesophytic old-growth forest in Kentucky. The volume of down wood at Schnabel Woods was more than twice that observed for a second-growth oak-hickory forest in southern Missouri (Shifley and others 1995).

While the total basal area and stocking at Schnabel Woods have remained constant over the last decade, this old-growth forest is changing in many ways. The dominant trees, red oaks in particular, continue to increase in size at the expense of trees in the lower canopy strata. Approximately 3% of the total number of trees die each year, but this mortality is offset by growth on surviving trees and by annual ingrowth which amounts to approximately 2% of the number of live stems. The conspicuous absence of oaks in the ingrowth portends a substantial change in the future species composition at Schnabel Woods. This future change in composition is further indicated by the size structure of the species that are present. Red, white, and chinkapin oaks, which currently make up 44% of the basal area, are virtually nonexistent in the lower crown classes. As seen most clearly in Figure 5, red oak is the most abundant species in the dominant crown class, and white oak and sugar maple share the remainder of the class. The codominant crown class is comprised predominantly of trees in the white oak and maple species groups. Over time, we expect the red oaks, which are faster growing and shorter-lived than the white oaks, to die and be replaced by the white oaks and maples currently in the codominant crown class. The white oaks will likely be a significant component of the overstory for a century or more, but in the absence of some dramatically altered disturbance regime, the sugar maples in the intermediate and overtopped crown classes will relentlessly move their way into dominance as individual oaks die. This suggested gradual pattern of increasing maple dominance is consistent with apparent patterns of forest change inferred from early surveyor records and with patterns of change in Schnabel Woods since the earlier inventory of Kucera and McDermott (1955). The oak domination of the Schnabel Woods overstory probably reflects past disturbance regimes (e.g. burning) more than present dynamics, which are driven by fine-scale treefall gaps.

Historically, fires in mixed mesophytic forests were found primarily on ridgetops or other restricted topographic positions (Runkle 1990). A prudent management plan for Schnabel Woods might include a careful reintroduction of fire on ridges to maintain shade intolerant species.

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METRIC CONVERSIONS

1 inch = 2.54 cm	1 ft ² = 0.092903 m ²	1 ft ³ = 0.028317 m ³	1 U.S. ton = 0.90718 metric tons
1 foot = 0.3048 m	1 ft ² /ac = 0.2296 m ² /ha	1 ft ³ /ac = 0.06997 m ³ /ha	1 U.S. ton/ac = 2.241 metric tons/ha
1 mile = 1.6093 km			